EUROPEAN WOODLAND AND FAUNA HISTORY

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Summary

European woodlands are poor in species. This is a result of a changing history of climate during the last two million years with a sequence of glacial and interglacial periods. During warm periods woodlands expanded, during cold eras they were restricted to small areas around the Mediterranean Sea. Big grazers among the fauna could spread, when grassland was available, but their areas were restricted by ice, which spread in cold phases, or woodland spreading in warmer eras.

After the last glacial phase woodland expanded again, like in earlier comparable periods. But it developed in another way as they were influenced by men. Mankind in Europe was involved by a nutritional crisis at the beginning of the Holocene, when dense woodlands developed and big grazers left the area. After some millennia they adopted agriculture. To practice agriculture woodlands were cleared. Wood and timber were important raw materials. Therefore they were not burnt, and swidden agriculture was not established as nowadays in tropical rainforests. As a solid economic structure was lacking settlements had to be shifted after some time to areas where timber was still available. Secondary successions could start on abandoned land. During secondary successions tree species expanded which were rare before, but rather characteristic to Europe of the present day, e.g. beech, spruce and hornbeam.

In Roman and Medieval times economic networks were established which allowed permanent settlement. It led to a much more intensive exploitation of woodlands than before and soon to an over-exploitation. Degradation of woodlands was progressing, and men had to think about reforms. Whereas some western European countries could import wood and timber from their colonies, in the inner parts of Europe the principle of sustainable forestry has been developed. It became possible to work with it after coal and oil could be exploited.

1. Introduction

Woodlands and their components, the flora, vegetation and fauna change through times. It is not only important to stress that components of ecosystems became more frequent or rarer in different periods. They changed also themselves. A familiar biological species of the present-day is an abstract item consisting of individuals. They are similar, but not equal. In the course of time, new individuals evolve. They are also similar, but not equal to their predecessors. Resulting from this it becomes clear that species are not constant items. The conditions of concurrence between groups of individuals, populations and species change through time. Dealing with history of flora and fauna, be it with concrete ecosystems like woodlands or be it with the vegetation in toto, it is always questionable from which point of time onwards one can talk about groups of individuals or their ecosystems which are comparable to those of the present-day. A country or a state, a family or dynasty has its specific history. These are objects which can be regarded as cultural constants. But if dealing with the history of species like beech or bear or with ecosystems like woodlands it must be stressed, that they were never constant. The history of a cultural constant "woodland" or "beech" is not relevant in a context of natural sciences. But also interesting cultural ideas are deriving from thinking like this.

Biological species of the present-day have only in common with their predecessors that they originate from them but they do not equal them. It is questionable from which point of time onwards ancient species and present-day species can be regarded at least as "similar". From the geological period of the Tertiary onwards, strains of the development of concrete ancient and present-day species are evident, so that the presentation of the history of vegetation and fauna in Europe should begin with this period.

2. Vegetation and Fauna of the Tertiary

The geological period of the Tertiary lasted from about 65 million years before present (B.P.) to about two million years B.P. During this period, the Alps and other high European mountains were formed such as the Pyrenees and the Carpathian mountains. Also the Mediterranean Sea became its present-day shape. It developed from an earlier larger sea, the Thetys, which was also extended to the region of the Alps and adjacent areas of southern and central Europe. Resulting from these geological processes Europe became its special character which was important to later developments of vegetation and fauna: There is a sea, the Mediterranean Sea between the continents of Africa, Asia and Europe, and there are high mountain chains, which are all orientated in a direction from west to east. They give a marked limitation to the south of the continent.

In the Tertiary not only angiosperms, the flowering plants, but also mammals and insects developed rapidly. All these groups spread to very many different ecological niches. They were able to grow or to live in very dry habitats such as deserts, but also in damp woodlands such as rain forests and, what is perhaps most important, also on sites which are seasonally dry or wet. Various flowering plants have very different flowers, and there are a lot of insects which developed in a co-evolution, so that they became specialized flower visitors.

During the Tertiary the mean temperatures in Europe declined gradually from about 20°C or more to about 10°C. This could have something to do with global phenomena but also with the continent's shift to the north. At the beginning of the period subtropical vegetation was wide-spread in Europe with very many species. Remnants of fossil palm trees are recorded from many sites, which are all dated to the early, but not the late Tertiary. This gives evidence for the decline of mean annual temperatures. Frost events became more frequent through time; palm trees cannot stand frost.

In sediments of the Tertiary, e.g. the following plant taxa were recorded as fossils: *Magnolia, Ficus* (fig), *Arbutus, Cinnamomum* (cinnamon tree) and other *Lauraceae, Citrus, Chamaecyparis, Taxus* (yew), *Taxodium, Pinus succinifera* (amber pine) and many others, which are generally distinct in Europe today or only occurring in restricted parts of the continent (e.g. *Arbutus unedo* on some sites in SW Ireland, some *Lauraceae* in the Mediterranean region). Also ancestors of species were present which are occurring in many parts of Europe today. Descendants of these taxa grow nowadays in several very different woodlands. This was possibly also the case in the Tertiary, but it must be noted, that the special conditions of concurrence between different tree taxa might have been very different from this of the present-day, so that it is possible that some tree taxa were occurring at the same stand which would not be possible today.

3. Vegetation and Fauna of the Quaternary

3.1. General Remarks

In the later Tertiary temperatures began to decline more and more rapidly. About two million years before present the Quaternary began, the period of the Ice Age. This was not only a cold era, but characterized by several changes of cold and warm periods. The cold eras are called glacial periods or simply "glacials", the warmer interglacial periods or interglacials. Glacials and interglacials are recorded by sediments if these were not destroyed by later geological processes. As many those records are removed it is not possible to state exactly into how many cold and warm phases the Quaternary was intersected. Classical Quaternary geology defined three to six glacial periods which were named after German rivers: the Danubian, the Günz Ice Age, the Mindel Ice Age, the Riss Ice Age and the Wurmian (or Würmian); in Northern Germany the Elster Ice Age, the Saalian and the Weichselian have been detected and defined. But later on several other cold phases, interrupted by warmer periods were detected. The parallelization of glacial sediments in different regions is not easy and still under debates. This is especially the case with older phases of the Quaternary. It is also not clear how many cold phases characterized the Quaternary. Perhaps there were between twenty and thirty glacial periods. In any case there were marked fluctuations of climatic conditions which are typical to this geological period. The climate was never stable for a longer period of time, and there were deviations of more than 10°C of the mean annual temperatures. It is necessary to deal with the general ecological effects of both cold and warm phases of the Quaternary, and with the effects of climate changes in general.

3.2. Cold and warm Phases of the Quaternary and Holocene

3.2.1. Cold Phases

In the cold phases, with a mean annual temperature which was in the range of about 10° C lower than today, there were severe winters and short summers. During the warmer season not all snow and ice smelted which were accumulated during winter. Snow was transformed to ice. In the course of time accumulations of ice became immensely extended so that they began to move – as glaciers. The largest glaciers originated in northern Europe, in Scandinavia and Finland. Smaller glaciers were formed in the Alps, the Pyrenees and the Carpathian mountains. All these mountain chains were formed in the geological era before, the Tertiary. There were also local glaciers in older mountainous areas such as the Black Forest and the Harz Mountains.

Large glaciers are very heavy and have extremely sharp edges. In the course of time they gave the routes on which they moved a special shape. U-shaped valleys were formed. They are now characterized by broad bottoms and steep slopes. Rocks were cut or broken from the bedrock. They were transported by the glaciers. During transport they became characteristic shapes: Edges were rounded so that pebble like rocks were generated, other stones were grinded to sand or even clay particles.

When glaciers expanded to other parts of the continent they transported rocks, sand and clay. More and more water was accumulated as ice in the glaciers, so that sea levels were lowered to more than 100 meters. In Europe, in a continent with a lot of flat coasts and adjacent shelf seas this had enormous consequences. The British Isles were than connected with the continent, the southern part of the North Sea basin was drained, the Mediterranean and the Black Sea were not connected, and many Mediterranean coasts had a markedly different position from the present-day state. Many parts of Europe were farther away from the coast than today so that the climate was not only colder but also more continental and drier than today. The increase of continental dryness was also caused by the fact that a lot of water was bound in the glaciers.

During the Ice Ages glaciers covered many parts of Europe. In some glacial periods glaciers from Scandinavia extended to England and Ireland, the northern part of Central Europe, to the Baltic region and to northern Russia. Together with the glaciers from the high mountains of Europe they influenced also the climate in their neighborhood. In most parts of Europe trees were not occurring. The trees of former woodlands starved or entire woodlands were destroyed. Deciduous and evergreen plants only survived at some places around the Mediterranean Sea where especially the winters were not as severe as in other parts of Europe; there frost rarely happened, so that some species demanding a mild climate could survive in these refugia.

On bright days even during glacial periods soils and the air near to the ground could be warmed by the sun, so that warmed air could rise inside the atmosphere. Resulting from this a low pressure area was generated in the area outside the glaciers. On the surface of the ice air was not rising, so that a high pressure area developed there. Resulting from this permanent cold winds were generated, blowing from the glaciers to adjacent areas. By this effect a cold climate was stabilized in Europe; the ice masses had the effect of extremely large refrigerators.

During summer times some ice melted; water was accumulated on the surface and at the bottom of the glaciers. Water from the bottom of the glaciers formed rivers running in the so called tunnel valleys under the ice and left the glaciers via gates at their fronts. Water transported pebbles, sand and clay as long as its streaming was strong enough. In the vicinity of the glaciers the force of the waters was lowered so that first pebbles, after this also sand particles were deposited on the ground as sediments, and a so-called sander (from the Icelandic word "sandúr") was formed. It contains a lot of sand, but also coarser particles. Water streams formed a broad valley parallel to the glacier front. During summer a lot of water was running there in the direction to the sea. Sand and clay were deposited on sites where the force of the water became lower so that even these small particles could not be transported any more.

During winters, when the ice was not melting, the sanders and the broad melt water valleys dried out. Ice was accumulated in the soils and let them bursting open when the ice was expanding. The permanent winds blowing from the glaciers to the adjacent areas met dry particles in the sanders and valleys and started to transport them. Dunes were formed from sand outside the valleys where the force of winds became lower. Clay particles were transported to hilly landscapes where they were deposited as loess. The clay particles contain all minerals which are demanded by plants such as potassium, magnesium and calcium. Later on very fertile stands could develop on loess.

In the cold peri-glacial areas only plants could grow which had a short development time. They had to grow rapidly when temperatures were high enough, and they had to develop flowers, seeds and fruits in a very short period. Among them there were many grass species and some herbs. They were not only adopted to low temperatures and a short growing season but also to drought caused by the fact that the precipitation rate was rather low. Therefore it is assumed that plants with the C4 metabolism of photosynthesis were rather wide-spread during cold phases of the Ice Age. Only plants with restricted root systems could survive. Plants with extended roots were destroyed by ice which was accumulated in the soil and spread during cold phases to burst not only parts of the soils but also the roots in them.

Animals spread which fed on grass and herbs. Large mammals such as reindeer, mammoth and wild horse migrated to the north in summer. Near to the glacier front there were a lot of sprouting plants with a low content of cellulose and a high content of proteins, which were a very attractive diet to such animals. Near to the glaciers there were also fewer mosquitoes than farther to the south. In winter many mammals migrated to the South because there was less snow, and still grass and herbs were available for grazing.

Reindeer can never stay in the same area for a long time, because their hooves destroy the soil cover and also the plants growing there. In the hoof marks seeds and fruits transported by wind could be "caught". Also air-transported clay could be collected in such marks, so that good seedbeds were formed, and new plants grew there in the following year. This process could only happen during a time-span when reindeer was not present. After grass and herbs had started to grow reindeer could return to feed on them again.

Grazing of animals like reindeer possibly allowed also the spreading of plants which did not occur at a stand before, but whose seeds or fruits had been transported to the site by the wind. Even species could start to grow which were not adapted to the specific climatic conditions. They were destroyed by drought or severe frost. But if climatic conditions had changed the "newcomers" could easily spread, and a vegetation succession could start.

During a cold phase of the Quaternary European trees could only survive in restricted areas with a mild climate. Some of the small woodlands formed by them were situated near to the Mediterranean coasts, the Black Sea coast and near to the Caucasus Mountains. Possibly some woodlands also existed in the extreme west of Europe, near to the Atlantic Ocean. Some conifers were possibly growing on special mild sites in Central Russia. These so-called Ice Age refugia were restricted by the Alps and the Mediterranean. They were smaller than on other continents with similar vegetation, in eastern Asia and western North America. Populations of tree species became very small because most of the individuals were destroyed by the climate or could not grow because of the concurrence to other tree species. The genetic variability of small populations is rather low; it can happen that it becomes too low to allow a spreading process after climatic conditions had become more convenient to the species again. During each cold phase of the Quaternary some tree species became therefore extinct, so that the biodiversity became smaller through the eras. Each cold phase might have caused the extinction of some species. This is important to the examination of the Quaternary stratigraphy. From era to era less tree species are recorded, so that they can be distinguished by their richness (early phase of the Quaternary) or their poorness (late phase of the Quaternary).

In eastern North America and eastern Asia tree species refugia of the Quaternary cold eras were not as restricted as in Europe. Many taxa from the species-rich Tertiary flora could survive the Ice Age there. Therefore deciduous woodlands of North America and eastern Asia, e.g. in China and Japan, have still a comparable composition as Tertiary woodlands, whereas European deciduous woodlands are characterized by their low number of tree species. But it is easy to bring many of these plants to Europe and plant them there; they can be found in very many parks and gardens, and some of them are still cultivated even in forests. It can be demonstrated by this fact that they did not become extinct by ecological conditions of special stands, but simply by passing e genetic bottle-neck in tree species refugia of the Quaternary.

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Biographical Sketch

Hansjörg Küster was born in Frankfurt/Main in 1956. He studied biology at Stuttgart-Hohenheim University and passed his diploma examination in 1981. He finished his doctoral thesis at the same university in 1985 and received a doctoral degree of a Dr.rer.nat. from the Faculty of Natural Sciences. From 1981 to 1998 he worked at the Institute for Pre-and Protohistory of Munich University, where he was the headed of the working group for vegetation history. In 1992, he received a habilitation degree of a Dr.rer.silv.habil. from the Faculty of Forestry Sciences of Munich University and became a Docent. He taught at several German universities (Potsdam, Regensburg, Würzburg, and Freiburg) in the fields of Biology, Forestry Sciences, Geography and Archaeology. In 1998 he became a Professor for plant ecology at the Institute for Geobotany at Leibniz University Hannover. Since 2004 he is also President of the Lower Saxonian Cultural Heritage Association.

He wrote several books, especially on landscape and its history, such as "Geschichte der Landschaft in Mitteleuropa" (3rd edition 1999), "Geschichte des Waldes (3rd edition 2008, Italian translation 2009), "Die Ostsee" (2nd edition 2004), "Die Elbe" (2007) and "Schöne Aussichten. Kleine Geschichte der Landschaft (2009).

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